



# New distributional records and rediscovery of three rare freshwater mussels (*Bivalvia*, *Unionidae*) in the Sequatchie River, Tennessee

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**Abstract.** We present new drainage records for five freshwater mussels in the Sequatchie River, a tributary of the Tennessee River. We also report the rediscovery of Purple Lilliput, *Toxolasma lividum* Rafinesque, 1831, Tennessee Pigtoe, *Pleuronaia barnesiana* (Lea, 1838), and the federally endangered Slabside Pearlymussel, *Pleuronaia dolabelloides* (Lea, 1840), and we provide information on other mussel species found in our survey. In the Sequatchie River, *T. lividum* was last seen in 1957 and *P. barnesiana* and *P. dolabelloides* were last seen in 1980. The discovery of five new drainage records and rediscovery of three rare species highlights the need for additional mussel surveys in the Sequatchie River and the importance of surveys in conservation efforts.

**Keywords.** Conservation easements, endangered, endemic mussels, extirpated species

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## Introduction

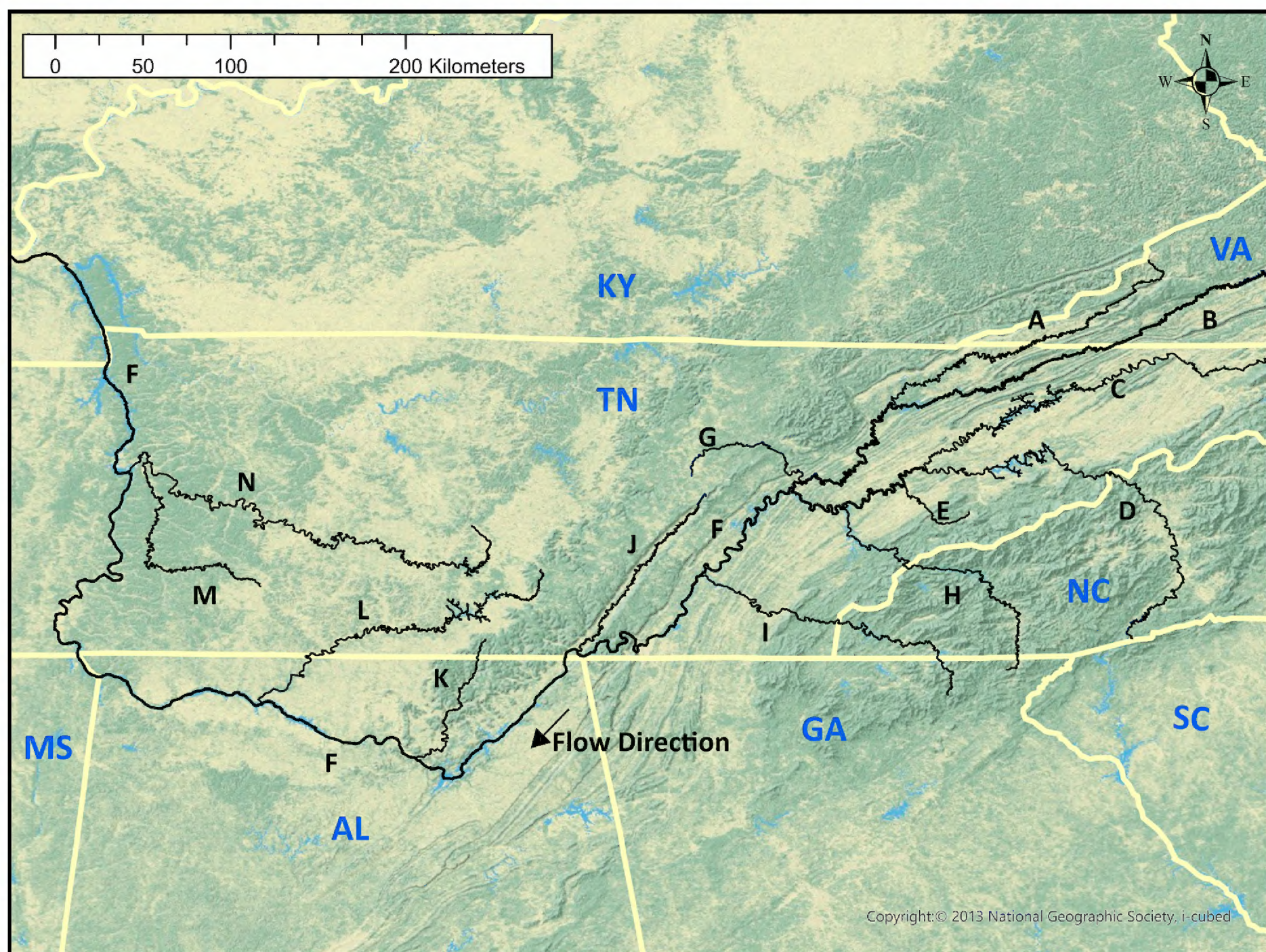
North America has the highest diversity of freshwater mussels in the world, and the freshwater and terrestrial gastropod fauna is among the richest (Johnson et al. 2013; Williams et al. 2017; Bouchet and Rocroi 2005). Interest in the taxonomy, distribution, and conservation of freshwater mussels (order Unionida, families Margaritiferidae and Unionidae) of the USA and Canada has increased over the last 50 years, due in part to the passage of the U.S. Endangered Species acts of 1966, 1969, and 1973 and the Canadian Species at Risk Act of 2002 (Williams et al. 2017). Recent research has shown approximately 74% of freshwater gastropods in these two countries are imperiled (Johnson et al. 2013), and the rate of imperilment in freshwater mussels is nearly identical (Jim Williams, U.S. Geological Survey, retired, unpubl. data). Within the USA, Alabama and Tennessee have the richest mussel faunas with approximately 190 species currently recognized in Alabama (Williams

et al. 2008) and 141 species recognized in Tennessee (G. Dinkins unpubl. data). These two states have lost the most mussel species to extinction (Alabama—22 species, Tennessee—16 species) (Williams et al 2008; Parmalee and Bogan 1998) and have the greatest number of mussels on the federal list of threatened and endangered species (Alabama—67, Tennessee—51) (U.S. Fish and Wildlife Service 2023).

With 104 species of freshwater mussels, the Tennessee River system is the most diverse in North America (Haag 2012). The Tennessee River begins in eastern Tennessee at the confluence of the French Broad and Holston Rivers and flows southwest into Alabama before turning west and northward and flowing into the Ohio River in western Kentucky. Its largest tributaries include the Clinch, Powell, Emory, Little, Little Tennessee, Hiwassee, Sequatchie, Paint Rock, Elk, Buffalo, and Duck Rivers (Fig. 1).

The earliest collection of mussels in the Sequatchie River drainage was by Ortmann (1925) who reported





**Figure 1.** Map of the Tennessee River drainage in Tennessee, Virginia, North Carolina, Georgia, Alabama, Mississippi, and Kentucky. Significant rivers are as follows: A = Powell, B = Clinch, C = Holston, D = French Broad, E = Little, F = Tennessee, G = Emory, H = Little Tennessee, I = Hiwassee, J = Sequatchie, K = Paint Rock, L = Elk, M = Buffalo, and N = Duck.

a total of 12 species from three locations on the main channel, one location on the Little Sequatchie River, and one location in an unnamed tributary. Hatcher and Ahlstedt (1982) reported 11 species at 10 sites in the lower reaches of the main channel. Gordon (1991) found 18 species at sites on the main channel and several tributaries and described the channel as being heavily silted and impacted by poor land-use practices. Gordon (1991) also found the river to be nearly devoid of mussels from km 72 to 128, with several species present only as relict shells or represented by only one or two living individuals. Since 1990, the Tennessee Valley Authority (TVA) has monitored water quality and the benthic macroinvertebrate community at eight fixed sites in the Sequatchie River between river km 11.4 and 179.1. Dead mussel shells found at these sites have occasionally been retained (Jeff Simmons, TVA, pers. comm.) and most are housed at the University of Tennessee's McClung Museum of Natural History and Culture (MMNHC).

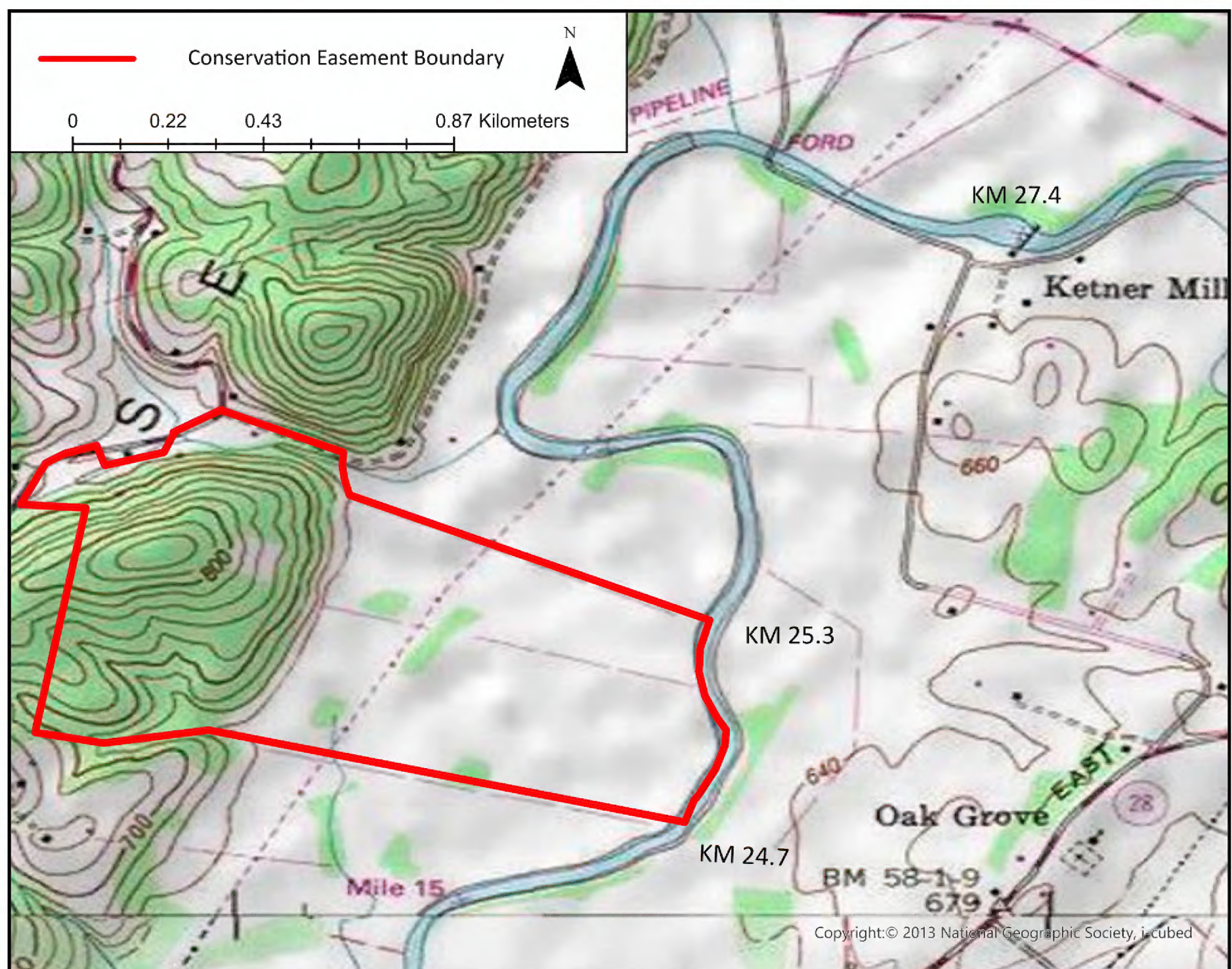
In 2018, a 73-ha tract of land bordering 1.7 km of the right descending bank of the Sequatchie River between river km 23.6 and 25.3 was placed into a permanent conservation easement. We were tasked with documenting the aquatic biodiversity in the wetlands and open water bodies on the parcel and in the main

channel of the Sequatchie River bordering the conservation easement property. Herein, we report the results of a survey of a short reach of the Sequatchie River, discuss five new drainage records and the rediscovery of three rare species, and provide recommendations for future research.

## Study Area

The Sequatchie River drains parts of Bledsoe, Cumberland, Grundy, Marion, Sequatchie, and Van Buren counties and originates from Head of Sequatchie Spring in Devilstep Hollow. From its source, the river flows southwest for 293 km to the confluence with the Tennessee River a few kilometers downstream of Walden Gorge, a geographic feature long recognized to be a distributional barrier to numerous mussel species (Ortmann 1918, 1925). The Sequatchie Valley remains narrow throughout its length (averaging less than 8 km wide) and divides Walden Ridge from the southern part of the Cumberland Plateau. Because of the narrow valley the Sequatchie River flows through, all tributaries are third order or smaller, except for the Little Sequatchie River, and most are small, spring influenced, and have a high to medium gradient. There are three low-head dams on the Sequatchie





**Figure 2.** Map showing the segment of Sequatchie River, Marion County, Tennessee surveyed for mussels in this study. Survey segment began at Ketner Mill, river km 27.4 and extended downstream to river km 24.7.

River, otherwise the main channel is free-flowing except for the lower 7.2 km which are impounded by Gunter'sville Reservoir. The towns of Pikeville, Dunlap, and Whitwell each have a permitted Wastewater Treatment Plant discharging to the Sequatchie River at river km 202.9, 113.8, and 59.5, respectively. There are several permitted mining facilities in the watershed, but all have been inactive for many years (Craig Walker, Office of Surface Mining, retired, pers. comm.). The Tennessee Department of Environment and Conservation (TDEC) considers the Sequatchie River between its confluence with the Tennessee River and the mouth of the Little Sequatchie River, along with several tributaries, to be "Exceptional Tennessee Waters" as defined by Rule Chapter 0400-40-3-06-4(a)3. However, this is because the lower reach of the Sequatchie River is designated as critical habitat for one or more populations of federally listed threatened or endangered aquatic animals, not because of exceptional water quality. In fact, TDEC considers segments of the Sequatchie River and several tributaries to be impaired by point and non-point source sedimentation, stream-side habitat alteration, high levels of *Escherichia coli*, and mercury (Hg) levels in fish tissue (TDEC 2023).

## Methods

On 7 July 2021 we investigated the Sequatchie River between Ketner Mill (river km 27.4) to the upstream boundary of the conservation easement property at river km 25.3 (Fig. 2). The purpose of the trip was to identify access points, assess depths, and determine equipment necessary for a subsequent and more substantial survey using a larger field crew. During this reconnaissance, fresh dead shells lying along the shoreline and on exposed surfaces were gathered. On 28 and 29 July 2021, we returned and conducted a series of searches for freshwater mussels in the Sequatchie River from km 24.7 to 25.3. In this reach, maximum depth was 4 m and the wetted width of the channel averaged 30 m. Substrates were dominated by gravel and cobble, with sand and boulders present. Underwater visibility averaged 2 m and flow averaged 5.1 m<sup>3</sup>/sec at the U.S. Geological Survey gage (No. 03571000) near Whitwell, Tennessee, approximately 15 river km upstream. Deeper areas (generally in the middle of the channel) were visually searched by two divers spaced 5–10 m apart using a surface supplied air system. Shallow margins were visually searched by a person on each side of the channel using a mask and snorkel. As the survey team progressed upstream, live mussels and dead



shells were removed from the substrate and temporarily held underwater in mesh bags. The survey team moved in unison and stopped periodically to identify and count live mussels and dead shells. Live mussels were measured to the nearest millimeter (long axis). Photographs were taken of live mussels before they were carefully reinserted into the substrate. Fresh dead shells were defined as those having traces of soft tissue remaining inside the shell or had lustrous nacre and an intact periostracum. Weathered dead and relict shells were combined and were defined as those without traces of soft tissue inside the shell, and with chalky or non-lustrous nacre and the periostracum mostly or entirely eroded. Most of the fresh dead shells and some relict shells encountered in the survey were cleaned, labeled, and catalogued at MMNHC. Additional photographs were taken in the museum of the species representing new drainage records. We follow the nomenclature of Williams et al. (2017), Watters (2018), and the Freshwater Mollusk Conservation Society checklist of names (2021), except we combined *Lampsilis cardium* Rafinesque 1820, Plain Pocketbook and *Lampsilis ovata* (Say, 1817), Pocketbook into a single taxon (*L. ovata*) for the reasons given by Williams et al. (2008). Fieldwork for this survey was conducted under permits issued to Gerald Dinkins (Tennessee Wildlife Resources Agency, Scientific Collecting Permit 1837, and U.S. Fish and Wildlife Service, Native Endangered and Threatened Species Recovery Permit TE069754-6).

To assess the historical record of mussels in the Sequatchie River, we searched files and the mollusk database at MMNHC, and we conferred with our colleagues at the U.S. Fish and Wildlife Service (USFWS), TVA, and the Tennessee Wildlife Resources Agency (TWRA). We utilized the InverteBase website (<https://invertebase.org/portal/>) to query other mollusk collections for records from the Sequatchie River, and we contacted the collection manager at The Ohio State University Museum of Biological Diversity (OSUM) and the North Carolina State Museum of Natural Sciences (NCSMNS) for information in their respective collections not available through InverteBase. We presumed all Sequatchie River specimens in these databases are correctly identified.

Results

In our survey of a short reach of the Sequatchie River, we found 438 live mussels and 464 dead shells representing 22 species from one order, Unionida, and one family, Unionidae (Table 1, Fig. 3). Dead shells were common on exposed surfaces between river km 25.3 and 27.4; most appeared to have been killed by muskrats. Between river km 24.7 and 25.3, live mussels and dead shells were evenly distributed and were present in all habitats.

TAXONOMY  
Class Bivalvia Linnaeus, 1758  
Order Unionida Gray, 1854

Family Unionidae Rafinesque, 1820

*Amblema plicata* (Say, 1817)

Threeridge

Figure 3A

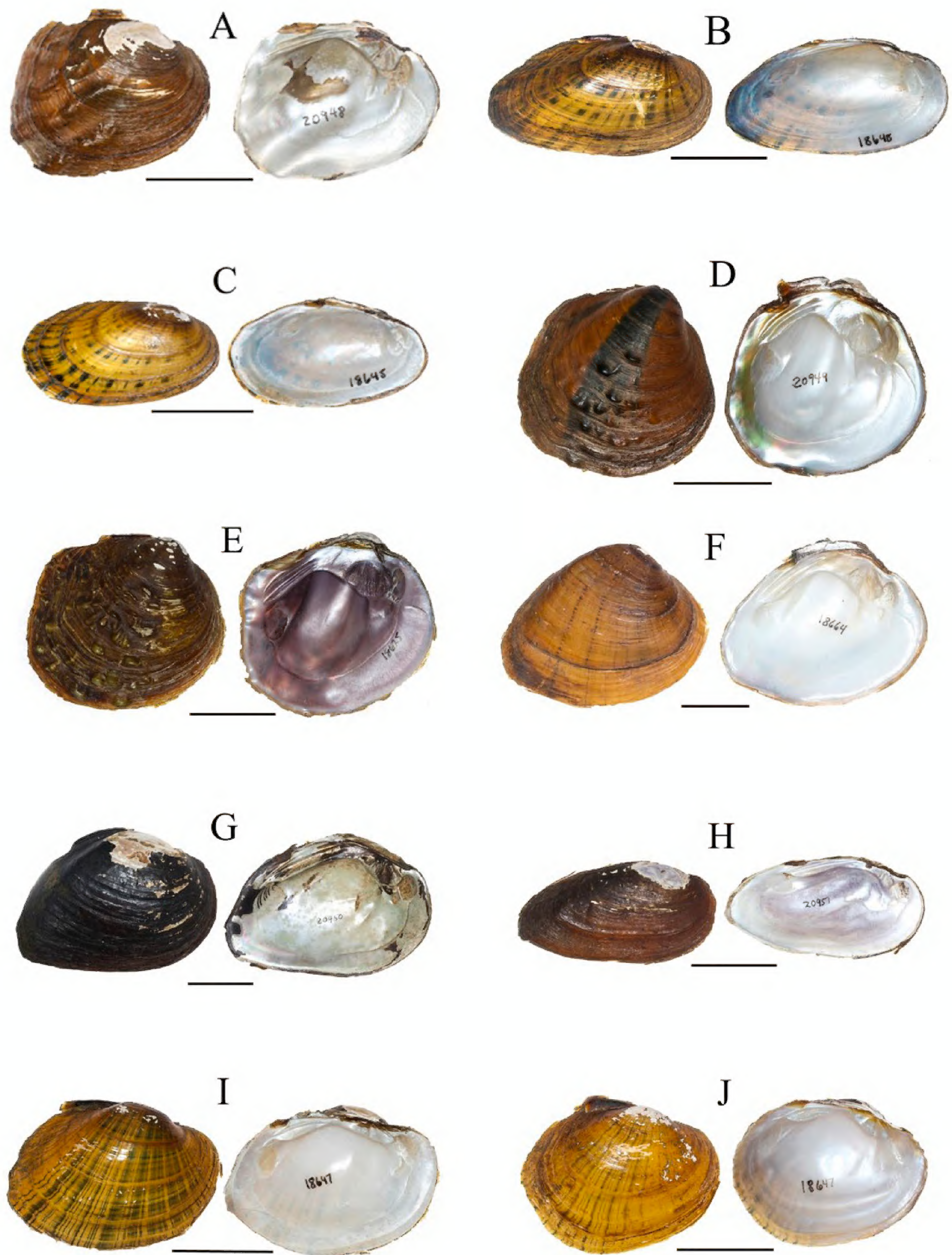
**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1299°N, –85.5235°W; river km 25.1; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 3 sex indeterminate (indet.), 45 mm MMNHC 20948.

**Identification.** We identified three dead *Amblema plicata* based on the dark periostracum, white nacre, solid and rounded shell outline, and medium size. Important diagnostic characters include the prominent beak and deep beak cavity. The exterior surface has several generally parallel ridges or folds emanating from the center of the shell and extending posteriorly. The pseudocardinal teeth are large, rough, and thick, the lateral teeth are moderately long and straight. *Amblema plicata* can be distinguished from *Megalonaias nervosa* (Rafinesque, 1820), Washboard, by its more rounded shape and the lack of sculpturing anteriorly to the umbo.

**Table 1.** Freshwater mussels found in the Sequatchie River, river km 24.7–27.4, Marion County, Tennessee, 7 and 28 July 2021. Number of live individuals followed by the number of fresh dead in parentheses and the combined number of relict and weathered dead shells in brackets. P = proposed; LE = Listed endangered.

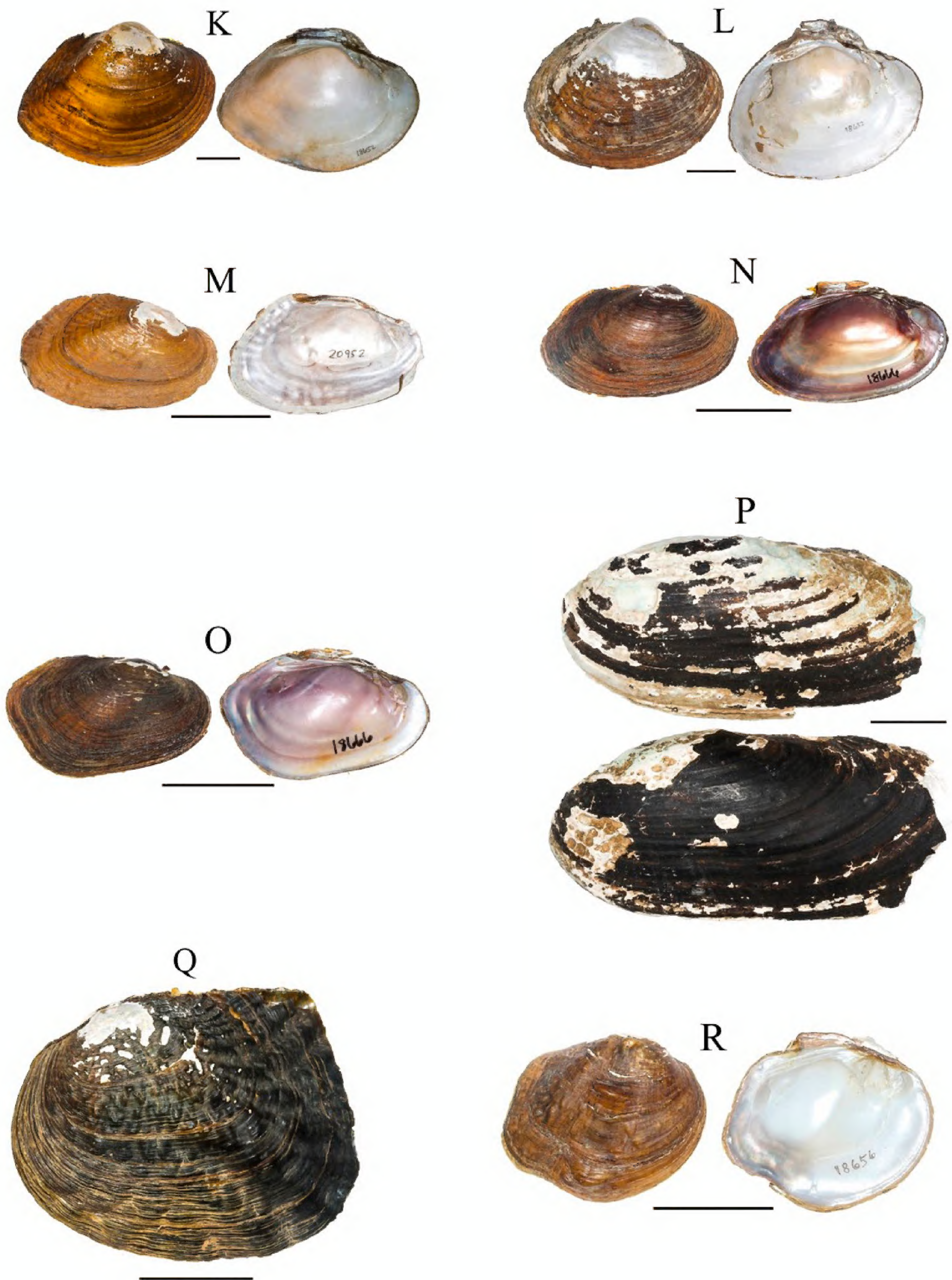
Species	Number collected	Federal status
<i>Amblema plicata</i>	(1) [2]	
<i>Cambarunio iris</i>	5 (42) [55]	
<i>Cyclonaias pustulosa</i>	27 (6) [25]	
<i>Cyclonaias tuberculata</i>	292 (32) [22]	
<i>Ellipsaria lineolata</i>	(1) [1]	
<i>Elliptio crassidens</i>	13[9]	
<i>Eurynia dilatata</i>	1 (1)	
<i>Lampsilis fasciola</i>	6 (4) [14]	
<i>Lampsilis ovata</i>	18 (2) [2]	
<i>Lasmigona costata</i>	4 (1)	
<i>Leaunio vanuxemensis</i>	4 (27) [46]	
<i>Ligumia recta</i>	[3]	
<i>Megalonaias nervosa</i>	3[1]	
<i>Obliquaria reflexa</i>	2 (4) [2]	
<i>Pleurobema cordatum</i>	1	
<i>Pleuronaia barnesiana</i>	3 (14) [1]	P
<i>Pleuronaia dolabelloides</i>	8 (1) [3]	LE
<i>Potamilus alatus</i>	5 (3) [3]	
<i>Ptychobranhus fasciolaris</i>	33 (8) [9]	
<i>Theliderma metanevra</i>	1	
<i>Toxolasma lividum</i>	12 (53) [61]	
<i>Tritogonia verrucosa</i>	(5)	
Total found:	438 (205) [259]	





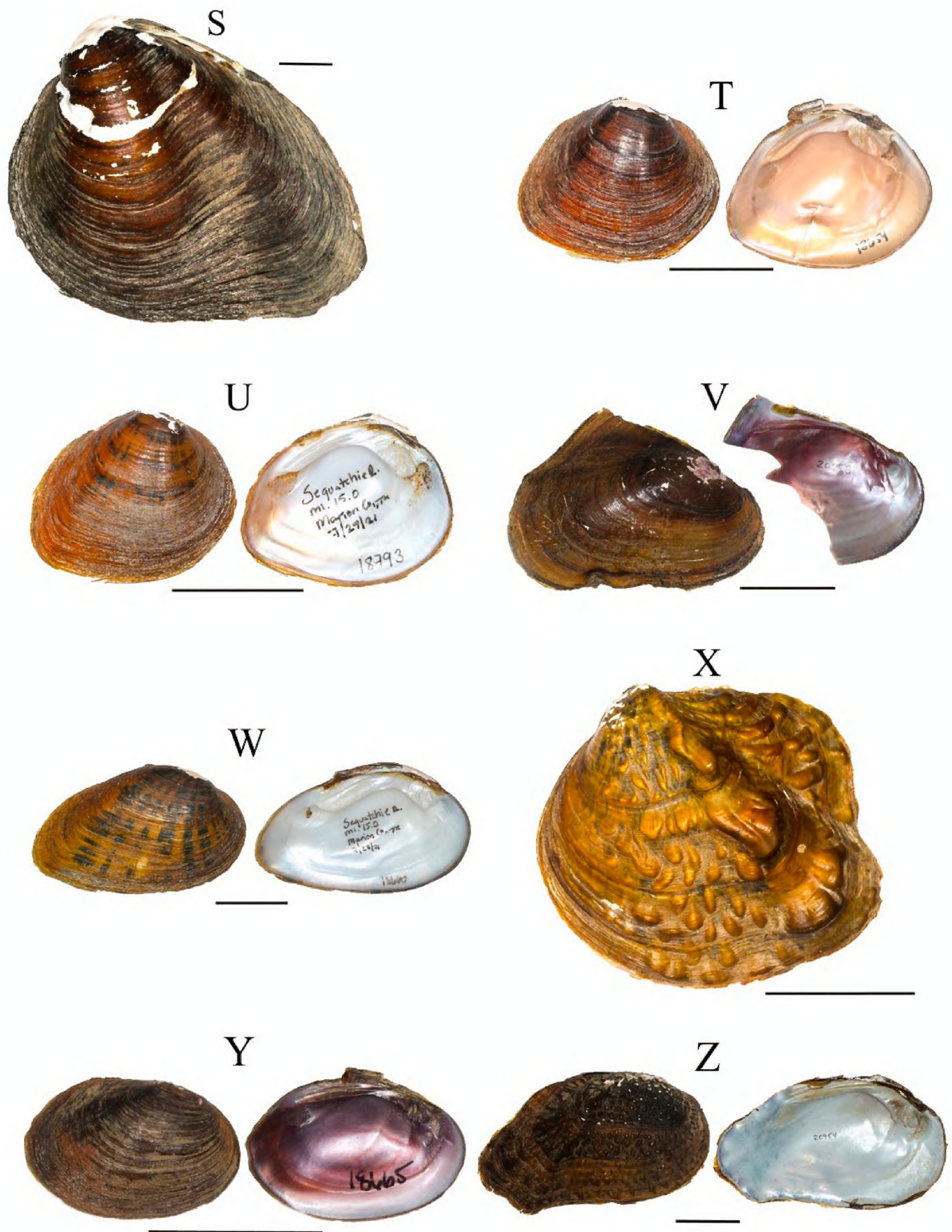
**Figure 3.** Freshwater mussels collected from Sequatchie River between river km 27.4 and 24.7. **A.** *Amblema plicata*. **B.** *Cambarunio iris* (male). **C.** *Cambarunio iris* (female). **D.** *Cyclonaias pustulosa*. **E.** *Cyclonaias tuberculata*. **F.** *Ellipsaria lineolata*. **G.** *Elliptio crassidens*. **H.** *Eurynia dilatata*. **I.** *Lampsilis fasciola* (male). **J.** *Lampsilis fasciola* (female). Scale bars = 25 mm [continued on next page].





**Figure 3** [continued]. Freshwater mussels collected from Sequatchie River between river km 27.4 and 24.7. **K.** *Lampsilis ovata* (male). **L.** *Lampsilis ovata* (female). **M.** *Lasmigona costata*. **N.** *Leaunio vanuxemensis* (male). **O.** *Leaunio vanuxemensis* (female). **P.** *Ligumia recta*. **Q.** *Megaloniaias nervosa*. **R.** *Obliquaria reflexa*. Scale bars = 25 mm [continued on next page].





**Figure 3** [continued]. Freshwater mussels collected from Sequatchie River between river km 27.4 and 24.7. **S.** *Pleurobema cordatum*. **T.** *Pleurobema barnesiana*. **U.** *Pleurobema dolabelliforme*. **V.** *Potamilus alatus*. **W.** *Ptychobranchius fasciolaris*. **X.** *Theliderma metanevra*. **Y.** *Toxolasma lividum*. **Z.** *Tritogonia verrucosa*. Scale bars = 25 mm.



**Geographical distribution.** *Amblema plicata* is widely distributed throughout the Mississippi River basin and its distribution extends northward into the Hudson Bay and Great Lakes (Dawley 1947; Burch 1975) and in the Gulf drainages from the Choctawhatchee River to the Nueces River (Williams et al. 2008). In Tennessee, *A. plicata* has been reported from nearly every major tributary to and the mainstem of the Tennessee and Cumberland Rivers and several of the direct tributaries to the Mississippi River. Gordon (1991) reported relict shells of *A. plicata* from five locations in the Sequatchie River and a single live individual from one location. The species typically occurs in gravel and sand substrates in shoals and pools of large creeks and rivers and can be found in reservoirs where there is current and firm substrates (Parmalee and Bogan 1998; Williams et al. 2008). Based on scarcity of live individuals found by Gordon (1991) and the lack of live individuals in our survey effort, the status of *A. plicata* in the Sequatchie River is uncertain.

**Comments.** Two relict single valves were not retained or measured due to their degraded condition.

***Cambarunio iris* (Lea, 1829)**

Rainbow

Figure 3B, C

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 26 ♂ 52–65 mm, 3 ♀ 41–45 mm, MMNHC 18653; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust leg.; 30 ♂ 41–74 mm, 7 ♀ 39–48 mm, MMNHC 18645.

**Identification.** We identified five live and 97 dead *Cambarunio iris* based on the small, thin shell that is elongate and compressed, and broadly rounded posterior and sharply rounded anterior ends, and straight to convex ventral margin. Important diagnostic characters include punctuated rays emanating from the beak and extending to or nearly to the ventral margin. Important internal shell characters include pseudocardinal teeth that are small and compressed, and lateral teeth that are thin and moderately short. The nacre color is variable. The species is distinguished from young *Ptychobranthus fasciolaris* (Rafinesque, 1820) by the thin shell and delicate lateral teeth.

**Geographical distribution.** The range of *Cambarunio iris* was revised by Watters (2018). It is reported to occur in tributaries to the Great Lakes, upper Ohio River basin, and the Tennessee River system above Tusculum, Alabama. In the Sequatchie River, Hatcher and Ahlstedt (1982) reported *Villosa taeniata* (Conrad, 1834) from two locations, and Gordon (1991) reported *Villosa nebulosa* from six locations. We assume specimens of *V. taeniata* reported by Hatcher and Ahlstedt (1982) and specimens of *V. nebulosa* reported by

Gordon (1991) represent *C. iris* based on their similarity in appearance.

**Comments.** Numerous relict specimens of *C. iris* were not retained due to their degraded condition.

***Cyclonaias pustulosa* (Lea, 1831)**

Pimpleback

Figure 3D

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 51 sex indet., 41–52 mm, MMNHC 20949; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust leg. 7 sex indet., 30–52 mm, MMNHC 18651.

**Identification.** We identified 27 live and 31 dead *Cyclonaias pustulosa* based on the solid, inflated, pustulose shell combined with the full, rounded beaks that exceed the shell outline. The periostracum is smooth and light brown. On small to medium-sized individuals, a squarish green bar expands ventrally from the beak. Important internal shell characters include heavy, triangular pseudocardinal teeth, short, curved lateral teeth, exceptionally deep beak cavity, and a pearly white nacre. *Cyclonaias pustulosa* is distinguished from *Cyclonaias tuberculata* (Rafinesque, 1820) by its white nacre and the presence of a green bar emanating from the beak.

**Geographic distribution.** *Cyclonaias pustulosa* is widely distributed from the eastern reaches of the Great Lakes, Lake St. Clair and Lake Erie, and through the Mississippi River Basin from western New York west to South Dakota (Parmalee and Bogan 1998; Williams et al. 2008) and south to Louisiana (Howells et al. 1996; Vidrine 1993). A recent genetic analysis by Johnson et al. (2018) expanded the range of *C. pustulosa* to include the Gulf Coast rivers from the Pascagoula River system in Mississippi west to the Nueces River system in southwest Texas. In Tennessee, *C. pustulosa* occurs in most medium-sized to large rivers (Parmalee and Bogan 1998). The species was not reported from the Sequatchie River by Hatcher and Ahlstedt (1982). Gordon (1991) reported finding relict shell of *C. pustulosa* at two locations. Our survey is the first to report live *C. pustulosa* in the Sequatchie River. Multiple size classes were observed.

**Comments.** Numerous fresh dead specimens of *C. pustulosa* were not retained because of the large number encountered.

***Cyclonaias tuberculata* (Rafinesque, 1820)**

Purple Wartyback

Figure 3E

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T.



Eldridge, B.M. Mize leg.; 292 sex indet., 26–82 mm, MMNHC 18625; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust leg. 22 sex indet., 28–60 mm, MMNHC 18661.

**Identification.** We identified 292 live and 54 dead *Cyclonaias tuberculata* based on the solid, somewhat compressed, pustulose shell combined with rounded beaks that barely exceed the shell outline. The periostracum is semi-glossy, light brown, and unrayed. Important internal shell characters include heavy, triangular pseudocardinal teeth, short, straight lateral teeth, exceptionally deep beak cavity, and a deep-purple nacre. *Cyclonaias tuberculata* is distinguished from *C. pustulosa* by its deep-purple nacre and the absence of a green bar emanating from the beak.

**Geographic distribution.** *Cyclonaias tuberculata* occurs in parts of the Great Lakes basin and is widespread in the upper and middle Mississippi River basin (Clarke 1981; Parmalee and Bogan 1998). In Tennessee, the species is found in the main channels of the Tennessee and Cumberland Rivers and in most of the major tributaries (Parmalee and Bogan 1998). The species was not reported by Hatcher and Ahlstedt (1982). Gordon (1991) reported relict shells of *C. tuberculata* at three locations and a live but very old individual at one location. *Cyclonaias tuberculata* was the most common species found in our survey and was represented by numerous size classes.

**Comments.** Numerous dead specimens of *C. tuberculata* were not retained because of the large number encountered.

#### ***Ellipsaria lineolata* (Rafinesque, 1820)**

Butterfly

Figure 3F

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 2 sex indet., 2 ♂ 68, 70 mm, MMNHC 18664.

**Identification.** We identified two dead *Ellipsaria lineolata* based on the heavy, compressed, subtriangular shell, light brown periostracum, presence of faint chevrons emanating from the beaks and terminating at the ventral margin, sharp posterior ridge, and medium size. Important diagnostic characters include the lack of a prominent beak and shallow beak cavity. The pseudocardinal teeth are triangular and heavy, the lateral teeth are short and curved, and the beak cavity is moderately deep. *Ellipsaria lineolata* can be distinguished from *Elliptio crassidens* (Lamarck, 1819) by its less elongated shell, sharp posterior ridge, presence of chevrons, and white nacre.

**Geographic distribution.** *Ellipsaria lineolata* is widespread in the Mississippi River basin, from Pennsylvania to Minnesota south to Ohio River basin (Simpson 1900; Parmalee and Bogan 1998) and in the Mobile

River basin in Alabama, Georgia, and Mississippi (Williams et al. 2008; Jones et al. 2021). In Tennessee, *E. lineolata* is widespread in the Tennessee and Cumberland Rivers and in several of their major tributaries. The species was not found by Hatcher and Ahlstedt (1982) and Gordon (1991) found only a single relict valve at one location. We found one relict valve and one fresh dead specimen, indicating the species is extant in the Sequatchie River but very rare.

#### ***Elliptio crassidens* (Lamarck, 1819)**

Elephantear

Figure 3G

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 22 sex indet., 96–140 mm, MMNHC 20950.

**Identification.** We identified 13 live and nine dead *Elliptio crassidens* based on the heavy, unrayed, subtriangular shell, dark brown to blackish periostracum, and medium to large size. Important internal shell characteristics include a shallow beak cavity, beaks that do not interrupt the shell outline, heavy pseudocardinal and lateral teeth, and faint to dark purple nacre. *Elliptio crassidens* can be distinguished from *Eurynia dilatata* (Rafinesque, 1820) by its slightly more inflated and heavier shell, more robust pseudocardinal teeth, and darker nacre.

**Geographic distribution.** *Elliptio crassidens* is widespread in the Mississippi River basin, south to Louisiana (Watters et al. 2009; Williams et al. 2008; Vidrine 1993). The species occurs in Gulf Coast drainages in Mississippi, Louisiana, Alabama, Georgia, and Florida (Jones et al. 2021; Williams et al. 2008; Vidrine 1993; Williams et al. 2014). In Tennessee, *E. crassidens* occurs in the Tennessee and Cumberland River drainages, and their larger tributaries, and in the Loosahatchie River in West Tennessee (Parmalee and Bogan 1998). In the Sequatchie River, the species was not found by Hatcher and Ahlstedt (1982), and Gordon (1991) found only a single relict valve at one location. We found 13 live individuals and nine relict shells. All were large individuals indicating the species may not be reproducing in the reach we surveyed.

#### ***Eurynia dilatata* (Rafinesque, 1820)**

Spike

Figure 3H

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 2 sex indet., 59–65 mm, MMNHC 20951.

**Identification.** We identified one live and one dead *E. dilatata* based on the compressed shell with a slight-



ly convex ventral margin, pointed posterior margin, and rounded anterior margin. Important diagnostic characters include lack of prominent beaks, and dark, cloth-like periostracum. *Eurynia dilatata* can be distinguished from *Ligumia recta* (Lamarck, 1819) by its more compressed shell and purple nacre.

**Geographical distribution.** *Eurynia dilatata* is distributed from the Great Lakes basin and St. Lawrence River, and in the Mississippi River basin south to northern Louisiana (Parmalee and Bogan 1998; Vidrine 1993). In Tennessee, the species occurs in small to large rivers throughout the Tennessee and Cumberland River systems (Parmalee and Bogan 1998). Live *E. dilatata* were found at multiple locations in the Sequatchie River by Hatcher and Ahlstedt (1982) and Gordon (1991).

### ***Lampsilis fasciola* Rafinesque, 1820**

Wavyrayed Lampmussel

Figure 3I, J

**Material examined.** UNITED STATES OF AMERICA – **Tennessee** • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 13 ♀ 51–60 mm MMNHC 18646; 35.14067°N, –85.52226°W; river km 27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust; leg.; 2 ♂ 58, 59 mm, 2 ♀ 51, 65 mm MMNHC 18647.

**Identification.** We identified six live and 18 dead *Lampsilis fasciola* based on the thin shell, medium size, glossy periostracum densely patterned with fine wavy lines that are not interrupted at the annual growth lines, and rounded beaks that break the shell outline. Important internal diagnostic characters moderate beak cavity, widely diverging pseudocardinal teeth, short, curved lateral teeth, and white or bluish-white nacre. *Lampsilis fasciola* can be distinguished from *Lampsilis ovata* (Say, 1817) by the presence of the wavy rays on the periostracum and the more rounded beak.

**Geographic distribution.** *Lampsilis fasciola* occurs in parts of the Great Lakes basin. The species occurs throughout the Ohio River basin but does not occur west of the Mississippi River (Watters et al. 2009). In Tennessee, *L. fasciola* occurs in small creeks to medium-sized rivers in the Tennessee and Cumberland River systems (Parmalee and Bogan 1998). Hatcher and Ahlstedt (1982) reported a single live *L. fasciola* and Gordon (1991) found relict shells at two locations and an unreported number of live individuals at one location. We found dead *L. fasciola* representing numerous size classes.

### ***Lampsilis ovata* (Say, 1817)**

Pocketbook

Figure 3K, L

**Material examined.** UNITED STATES OF AMERICA – **Tennessee** • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T.

Eldridge, B.M. Mize leg.; 20 sex indet.; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust leg. 1 ♂ 111 mm, 1 ♀ 100 mm, MMNHC 18652.

**Identification.** We identified 18 live and four dead *L. ovata* based on the glossy yellow periostracum, thin and oval shell outline, convex ventral margin, inflated beaks, defined posterior ridge, and medium to large size. Important internal shell characters include well developed pseudocardinal teeth, short, curved lateral teeth, open and deep beak cavity, and white nacre. *Lampsilis ovata* can be distinguished from *L. fasciola* by the lack of rays on the periostracum and a higher, more full inflated beaks.

**Geographical distribution.** *Lampsilis ovata* occurs in most of the Ohio River basin (Strayer and Jerka 1997; Cummings and Mayer 1992; Williams et al. 2008). In Tennessee, the species is found throughout the Tennessee and Cumberland River systems and in the direct tributaries to the Mississippi River (Parmalee and Bogan 1998). Live, fresh dead, or relict *Lampsilis ovata* were reported by Hatcher and Ahlstedt (1982) at several locations in the Sequatchie River, and Gordon (1991) reported relict shells of *L. cardium/ovata* at four locations. We found live individuals of *L. ovata* representing several size classes.

### ***Lasmigona costata* (Rafinesque, 1820)**

Flutedshell

Figure 3M

**Material examined.** UNITED STATES OF AMERICA – **Tennessee** • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 4 sex indet., 100–130 mm, MMNHC 20952.

**Identification.** We identified four live and one dead *Lasmigona costata* based on the medium-sized, compressed shell with greenish periostracum, beaks that do not break the shell outline, and distinct plications radiating from the posterior ridge to the posterior margin. *Lasmigona costata* can be distinguished from *Tritogonia verrucosa* (Rafinesque, 1820) by the lack of sculpturing on the shell anterior to the posterior ridge, lack of a sulcus, and by having a posterior ridge that is not inflated ventrally.

**Geographical distribution.** *Lasmigona costata* is widespread, occurring in the Great Lakes basin and Hudson River system, and the entire Mississippi River basin from Minnesota south to Arkansas (Clarke 1985). In Tennessee, it occurs in small to medium-sized tributaries to, and the main channel of, the Tennessee and Cumberland Rivers (Parmalee and Bogan 1998). The species was not found in the Sequatchie River by Hatcher and Ahlstedt (1982), and Gordon (1991) found only relict valves at five locations.



***Leaunio vanuxemensis* (Lea, 1838)**

Mountain Creekshell

Figure 3N, O

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 6 ♂ 48–65 mm MMNHC 18662; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust leg. 11 ♂ 43–58 mm, 9 ♀ 41–57 mm MMNHC 18666.

**Identification.** We identified four live and 73 dead *L. vanuxemensis* based on the dark periostracum, elongate/elliptical shell outline, and small size. Important diagnostic characters include the presence of faint, thin rays on the posterior half of the shell, lack of a prominent beak, shallow beak cavity, and bronze to purple nacre. The pseudocardinal teeth are small and triangular and the lateral teeth are thin, short, and straight. *Leaunio vanuxemensis* is strongly dimorphic. Female shells are more inflated and have a biangulate posterior margin, while male shells have a narrowly rounded posterior margin. The species can be distinguished from *Eurynia dilatata* by its more inflated and thinner shell, and its strong dimorphism. *Leaunio vanuxemensis* can be distinguished from *C. iris* by having rays restricted to the posterior half of the shell, darker periostracum, and bronze to purple nacre.

**Geographical distribution.** *Leaunio vanuxemensis* is widely distributed in the Tennessee, Duck, and Cumberland River systems of Virginia, North Carolina, Tennessee, Georgia, Alabama, Mississippi, and Kentucky (Parmalee and Bogan 1998; Williams et al. 2008; Watters 2018; Jones et al. 2021). In Tennessee, *L. vanuxemensis* is found in small creeks to medium rivers, although it is more common in headwaters (Parmalee and Bogan 1998). Hatcher and Ahlstedt (1982) reported a single live individual at one main channel location in the Sequatchie River, and Gordon (1991) found live and relict valves of *L. vanuxemensis* at three locations each in the main channel of the Sequatchie River.

**Taxonomic remarks.** *Leaunio vanuxemensis* is currently the subject of range-wide molecular analysis to determine its relationship and distribution relative to other species of *Leaunio*, especially *Leaunio ortmanni* (Walker, 1925) (Kuehn 2009; Watters 2018; Jess Jones, USFWS, pers. comm.).

**Comments.** Numerous dead specimens of *L. vanuxemensis* were not retained because of the large number encountered.

***Ligumia recta* (Lamarck, 1819)**

Black Sandshell

Figure 3P

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021;

G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 2 ♂, 120, 130 mm, MMNHC 18634.

**Identification.** We identified three dead *Ligumia recta* based on the dark periostracum, solid and elongate/elliptical shell outline, and medium to large size. Important diagnostic characters include the lack of a prominent beak and shallow beak cavity. The pseudocardinal teeth are triangular, the lateral teeth are elongate and straight, and the pallial line is impressed anteriorly. *Ligumia recta* can be distinguished from *Eurynia dilatata* by its more inflated shell, thicker pseudocardinal teeth, and white nacre.

**Geographical distribution.** *Ligumia recta* is widely distributed throughout the Mississippi River basin and its distribution extends northward into the St. Lawrence River system (Parmalee and Bogan 1998). On the Gulf Slope, *L. recta* occurs in the Mobile River Basin of Alabama and Mississippi and the Pearl River basin in Mississippi and Louisiana (Williams et al. 2008; Jones et al. 2021). In Tennessee, *L. recta* has been reported from nearly every major tributary to and the mainstem of the Tennessee and Cumberland Rivers and has been reported from the Tennessee River a few km downstream of the mouth of the Sequatchie River (Parmalee and Bogan 1998). The species typically occurs in medium-sized to large rivers where there is strong current and coarse sand and gravel with cobble and depths from a few centimeters to two or more meters (Parmalee and Bogan 1998). We retained two single valves of this species and catalogued them at the MMNHC collection. Based on the lack of live individuals in our survey effort, the status of *L. recta* in the Sequatchie River is uncertain.

**Comments.** Length of two relict left valves in Figure 18 is estimated due to posterior tip missing in both specimens; a third relict valve (sex indet.) was not measured or retained due to its degraded condition.

***Megaloniais nervosa* (Rafinesque, 1820)**

Washboard

Figure 3Q

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1298°N, –85.5233°W; river km 24.9; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 4 sex indet., 113–140mm; 1 single valve sex indet., 137 mm.

**Identification.** We identified three live and one dead *M. nervosa* based on the dark periostracum, solid and quadrate shell outline, and large size. Important diagnostic characters include the shell surface which is mostly covered with nodulous plications and the beaks which are narrow and do not exceed the outline of the hinge line. There are two heavy pseudocardinal teeth and two slightly curved lateral teeth in the left valve of the relict specimen we found. The species is distinguished from *Amblema plicata* by its more quadrate shape and the presence of sculpturing anteriorly to the umbo.



**Geographical distribution.** *Megalonaias nervosa* is widespread throughout the Mississippi River basin and inhabits the Gulf drainages from the Ochlockonee River west to the Rio Grande River (Parmalee and Bogan, 1998). In the Tennessee River system, *M. nervosa* ranges from eastern Tennessee downstream to the confluence with the Ohio River (Parmalee and Bogan 1998; Haag and Cicerello 2016). The species can inhabit large creeks but is more common in large rivers and can be found at depths approaching 20 m (Williams et al. 2008). The presence of at least two size classes in the live individuals we found suggests the species is rare but reproducing in the Sequatchie River.

***Obliquaria reflexa* (Rafinesque, 1820)**

Threehorn Wartyback

Figure 3R

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 4 sex indet. 27–37 mm; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust leg. 4 sex indet. 39–48 mm MMNHC 18656.

**Identification.** We identified two live and six dead *Obliquaria reflexa* based on the solid, somewhat inflated, oval shell with dark, cloth-like periostracum and full beaks that break the outline of the shell. Important diagnostic characters include a sharp posterior ridge usually having a series of parallel, subtle plications, and a row of 3–5 large knobs emanating from the beak to the ventral margin; the knobs on one valve alternate in position with the knobs on the other valve. The nacre is pearly white. *Obliquaria reflexa* is distinguished from *Theliderma metanevra* (Rafinesque, 1820) by the dark periostracum, lack of knobs on the posterior ridge, and presence of knobs on the central part of the shell that alternate between the valves.

**Geographical distribution.** *Obliquaria reflexa* occurs in Lake Erie and its tributaries and is widespread in the Mississippi River basin from Minnesota south to Louisiana (Williams et al. 2008). The species also occurs in several Gulf Coast drainages from Florida to Texas (Williams et al. 2008). In Tennessee, *O. reflexa* occurs throughout the Tennessee and Cumberland River systems (Parmalee and Bogan 1998). The species was not found in the Sequatchie River by Hatcher and Ahlstedt (1982) or Gordon (1991). There is only one previous record of the species from the Sequatchie River: seven specimens collected August 1957 at Ketner Mill (Harvard University Museum of Comparative Zoology, Catalog Number 236180).

***Pleurobema cordatum* (Rafinesque, 1820)**

Ohio Pigtoe

Figure 3S

**Material examined.** UNITED STATES OF AMERICA

– Tennessee • Sequatchie River, Marion County; 35.1299°N, –85.5235°W; river km 25.1; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 1 sex indet., 93 mm.

**Identification.** We identified one live *Pleurobema cordatum* based on the semi-dark and cloth-like periostracum, heavy and smooth shell with subtriangular outline, and bluntly pointed anterior shell margin. The individual had a wide, shallow sulcus anterior to the broad posterior ridge. Important diagnostic characters include the cloth-like shell surface and the round, full beaks which break the shell outline and are angled anteriorly. *Pleurobema cordatum* is distinguished from *Pleuonaia barnesiana* (Lea, 1838) and *P. dolabelloides* (Lea, 1840) by the high, full umbos, wide and shallow sulcus, and dark, unrayed periostracum.

**Geographical distribution.** *Pleurobema cordatum* occurs in the upper Mississippi and St. Lawrence River basins (Parmalee and Bogan 1998; Watters et al. 2009). The species is found in medium-sized to large rivers, where it occurs in flowing water with substrates composed of mixtures of sand and gravel (Williams et al. 2008). We found one live individual at the upper end of our study reach at 1 m depth in the center of the channel indicating the species is present but rare in the Sequatchie River.

**Taxonomic remarks.** *Pleurobema cordatum*, *P. clava* (Lamarck, 1819), *P. plenum* (Lea, 1840), and *P. rubrum* (Rafinesque, 1820) are currently the subject of range-wide molecular analysis to determine their relationship and distribution (Nathan Johnson, U.S. Geological Survey, pers. comm.). Ortmann (1925) reported specimens of *Pleurobema clava* (Lamarck, 1819) in the Bryant Walker collection from the Sequatchie River at Jasper. Parmalee and Bogan (1998) reported *P. clava* formerly occurred in the Sequatchie River although this appears to be based on Ortmann's record, as we could find no specimens of this species in any of the collections we queried. Based on these findings, we do not consider *P. clava* to have historically occurred in the Sequatchie River.

***Pleuonaia barnesiana* (Lea, 1838)**

Tennessee Pigtoe

Figure 3T

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize 12 sex indet., 39–43 mm, MMNHC 18655; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust, 6 sex indet., 33–45 mm, MMNHC 18654.

**Identification.** We identified three live and 15 dead *P. barnesiana* based on the semi-glossy and light brown periostracum, umbos that do not break the shell outline, and its quadrate outline. Important diagnostic characters include pseudocardinal teeth that are compressed



and nearly parallel. Most individuals we encountered had distinct or faint greenish rays. There is no flattened, plate-like area ending at the posterior ridge, and live individuals have a creamy white or tan foot.

**Geographical distribution.** *Pleuronaia barnesiana* is endemic to the Tennessee River drainage (Simpson 1914) where it occurs in medium-sized creeks and rivers in eastern and middle Tennessee (Parmalee and Bogan 1998). The species typically occurs in moderate current at depths less than 1 m, and in substrate composed of coarse sand, silt, and gravel. Based on the number of live and fresh dead shells encountered in our survey, the species is reproducing in the Sequatchie River downstream of Ketner Mill.

***Pleuronaia dolabelloides* (Lea, 1840)**

Slabside Pearlymussel

Figure 3U

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1299°N, –85.5235°W; river km 25.1; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize 12 leg.; sex indet. 35–81 mm, MMNHC 18793

**Identification.** We identified eight live and four dead *P. dolabelloides* based on the semi-glossy and light brown periostracum, full umbos that slightly break the shell outline, and the presence of broad, interrupted greenish rays extending from the umbos diagonally to the ventral margin of the shell. There is a flattened, plate-like area ending at the posterior ridge. Important internal shell characters include triangular pseudocardinal teeth bordered by a broad interdentum, shallow beak cavity, and pearly white nacre. *Pleuronaia dolabelloides* can be distinguished from *P. barnesiana* and *Pleurobema oviforme* (Conrad, 1834) by its ventrally curved posterior ridge which forms the posterior border of a flattened plate and by its bright orange foot (Williams et al. 2008).

**Geographical distribution.** *Pleuronaia dolabelloides* is endemic to the Cumberland and Tennessee river drainages (Parmalee and Bogan 1998; Williams et al. 2008). Historically, the species occurred in large creeks to large rivers in shoal habitat consisting of sand, fine gravel, and cobble substrates (Parmalee and Bogan 1998). Based on the number of live and fresh dead shells encountered in our survey, the species is common and reproducing in the Sequatchie River downstream of Ketner Mill.

***Potamilus alatus* (Say, 1817)**

Pink Heelsplitter

Figure 3V

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T.

Eldridge, B.M. Mize leg.; 8 sex indet. 28–117 mm, MMNHC 20953; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust leg. 1 sex indet. 101 mm, MMNHC 18658.

**Identification.** We identified five live and six dead *P. alatus* based on the moderately thick, compressed, and ovate shell having a straight ventral margin, high posterior wing, and small beaks that do not break the shell outline. The periostracum is light to dark brown. Important internal shell characters include sharp, triangular pseudocardinal teeth, long, slightly curved lateral teeth, shallow beak cavity, and a dark purple nacre. *Potamilus alatus* is distinguished from *Lampsilis ovata* by its more compressed shell, dark brown periostracum, presence of a high wing, and purple nacre.

**Geographical distribution.** *Potamilus alatus* occurs in the Great Lakes basin and St. Lawrence River system, throughout the Mississippi River basin south to Arkansas and Tennessee (Parmalee and Bogan 1998; Williams et al. 2008). In Tennessee, the species is widespread, occurring widely in the main channel of the Tennessee and Cumberland Rivers and in medium-sized to large tributaries (Parmalee and Bogan 1998). We found the species to be common throughout our survey reach with numerous age classes represented indicating the species is common and reproducing in the Sequatchie River downstream of Ketner Mill.

***Ptychobranhus fasciolaris* (Rafinesque, 1820)**

Kidneyshell

Figure 3W

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 4 sex indet. 53–73 mm, MMNHC 18660; 35.14067°N, –85.52226°W; river km 24.9; 7.VII.2021; B.J. Dinkins, H.D. Faust leg.; 33 sex indet. 12–103 mm, MMNHC 18657.

**Identification.** We identified 33 live individuals and 17 dead *P. fasciolaris* based on the solid, elongate, elliptical, and compressed shell combined with a bluntly pointed posterior end and a rounded anterior end, and umbos that do not exceed the shell outline. The periostracum is light brown and most of the specimens we encountered had wide, interrupted rays. Important internal shell characters include heavy, triangular pseudocardinal teeth, short, straight lateral teeth, exceptionally shallow beak cavity, and a pearly white nacre. *Ptychobranhus fasciolaris* is distinguished from *Eurynia dilatata* by its more inflated shell, brownish periostracum, and white nacre.

**Geographical distribution.** *Ptychobranhus fasciolaris* occurs in the Ohio River basin and the Great Lakes basin (Watters et al. 2009). In the Tennessee River, the species historically occurred downstream to the confluence with the Ohio River (Parmalee and Bogan 1998; Haag and Cicerello 2016). The species occurs in small



to large rivers, typically in habitats with flowing water where there is sand and gravel (Williams et al. 2008). In the main channel of the Tennessee River, *P. fasciolaris* can be found at depths exceeding 6 m (Williams et al. 2008). We found the species to be common throughout our survey reach with numerous age classes represented indicating the species is reproducing downstream of Ketner Mill.

***Theliderma metanevra* (Rafinesque, 1820)**

Monkeyface

Figure 3X

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1290°N, –85.5231°W; river km 24.9; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize 1 leg.; sex indet., 86 mm.

**Identification.** We identified one live *T. metanevra* based on the solid, inflated, and square-shaped shell, and umbos that slightly exceed the shell outline. The periostracum is brown, smooth, and unrayed. Important diagnostic characters include an inflated posterior ridge that extends diagonally from the umbos toward the posterior ventral margin and the presence of several large, elevated knobs. *Theliderma metanevra* can be distinguished from *Theliderma cylindrica* (Say, 1817) by its square-shaped shell, inflated posterior ridge, and presence of large, elevated knobs.

**Geographical distribution.** *Theliderma metanevra* occurs in the upper and middle Mississippi River basin south to the Ouachita River in Louisiana (Williams et al. 2008; Vidrine 1993). The species is found in medium-sized to large rivers in flowing water, in substrates comprised of sand and gravel (Williams et al. 2008). The collection of a live individual in our survey indicates the species is present but very rare in the Sequatchie River downstream of Ketner Mill.

***Toxolasma lividum* Rafinesque, 1831**

Purple Lilliput

Figure 3Y

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1290°N, –85.5235°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 7 ♂ 24–45 mm, 4 ♀ 33–42 mm, 1 sex indet., MMNHC 18665; 35.14067°N, –85.52226°W; river km 25.3–27.4; 7.VII.2021; B.J. Dinkins, H.D. Faust; leg.; 5 ♂ 27–35 mm, 4 ♀ 26–30 mm, MMNHC 18663.

**Identification.** We identified 12 live and 114 dead *Toxolasma lividum* based on the dark, cloth-like and unrayed periostracum, small shell size, rounded shell anterior, and nearly straight ventral shell margin. Males are characterized by the short and elliptical shell outline, while females are distinctly inflated. Important internal shell characters include a bright purple nacre and erect, triangular pseudocardinal teeth and nearly

straight lateral teeth. *Toxolasma lividum* can be distinguished from *Toxolasma parvum* (Barnes, 1823) by its heavier shell and purple nacre.

**Geographical distribution.** *Toxolasma lividum* occurs in the Mississippi River basin only in the Ouachita and Ozark highlands (Haag and Cicerello 2016) and in the Ohio River basin (Parmalee and Bogan 1998; Watters et al. 2009). This diminutive species is found in medium-sized rivers in mud, sand, and gravel substrates but is most common in small to medium-sized streams (Haag and Cicerello 2016, Watters 2009). Like several other species of *Toxolasma*, it is often found along stream margins and in depositional areas (G. Dinkins, personal observation) and may live 12 years (Watters et al. 2009). Our collection of numerous live and fresh dead *T. lividum* represented by several size classes indicates the species is abundant and reproducing downstream of Ketner Mill.

**Comments.** In addition to the 44 fresh dead *T. lividum* found between river km 25.3 and 27.4, we collected 61 relict specimens that were not retained.

***Tritogonia verrucosa* (Rafinesque, 1820)**

Pistolgrip

Figure 3Z

**Material examined.** UNITED STATES OF AMERICA – Tennessee • Sequatchie River, Marion County; 35.1267°N, –85.5244°W; river km 24.7–25.3; 28.VII.2021; G.R. Dinkins, B.J. Dinkins, H.D. Faust, R.T. Eldridge, B.M. Mize leg.; 5 sex indet., 85 mm, MMNHC 20954.

**Identification.** We identified five dead *T. verrucosa* based on the solid, elongate shell sculptured with numerous nodules and plications across both valves, a distinct, elevated posterior ridge, and a greenish/brown periostracum. Important internal shell characters include a pearly white nacre, moderately deep beak cavity, thick pseudocardinal teeth, and short, straight lateral teeth. *Tritogonia verrucosa* can be distinguished from *Theliderma metanevra* by its elongate shell, lack of large knobs on the posterior ridge, and greenish periostracum.

**Geographical distribution.** *Tritogonia verrucosa* is widely distributed throughout the Mississippi River basin, from the upper reaches of the Ohio River basin south to Louisiana (Watters et al. 2009; Williams et al. 2008; Vidrine 1993). In Tennessee, the species occurs statewide, except for the upper Tennessee River system (Parmalee and Bogan 1998). In the Sequatchie River, *T. verrucosa* was not reported by Hatcher and Ahlstedt (1982), and Gordon (1991) found only a relict valve at a single location. Based on the lack of live individuals in our survey, the status of *T. verrucosa* in the Sequatchie River downstream of Ketner Mill is uncertain.

**Comments.** In addition to the one fresh dead specimen collected and retained between river km 24.7–25.3, we collected four fresh dead specimens from this reach that were not retained or measured.



Discussion

A search of the InverteBase website (<https://invertebase.org/portal>) for mussels found in the Sequatchie River revealed 29 records representing 23 species, all collected prior to the late 1950s and all from Sequatchie and Marion counties (Table 2). These records are in the collections at the Denver Museum of Nature and Science, Florida Museum of Natural History, Harvard University Museum of Comparative Zoology, NCS-MNS, and the University of Michigan Museum of Zoology. An additional 18 records from the Sequatchie River between 1909 to 1991 but not available in InverteBase were provided to us by NCSMNS, and the online mollusk database at OSUM contains four records representing three species collected between 1965 and 1981. In the mollusk collection at MMNHC there are 30 records representing 12 species collected between 1973 and 2017. Based on current taxonomy, these museum records document a total of 39 mussel species historically occurring in the Sequatchie River drainage.

Herein we report new drainage records for *Ligumia recta*, *Megaloniaias nervosa*, *Pleurobema cordatum*, *Ptychobranchnus fasciolaris*, and *Theliderma metanevra*. All five species were known to historically occur in the Tennessee River near the confluence with the Sequatchie River. *Ligumia recta* was recorded in the early 1900s from the Tennessee River at Bridgeport, approximately

13 km downstream of the Sequatchie River (UMMZ 098316). *Megaloniaias nervosa* was recorded in 1980 from the Tennessee River near the downstream end of Burns Island, approximately 3.1 km downstream from the Sequatchie River (MMNHC 5456). *Pleurobema cordatum* was recorded in 1999 from the Tennessee River approximately 2 km upstream from the Sequatchie River (Illinois Natural History Survey 24596, NCS-MNS 47689). *Ptychobranchnus fasciolaris* was recorded in 1999 in the Tennessee River approximately 2 km upstream from the Sequatchie River (Illinois Natural History Survey 24599; NCSMNS 47709). *Theliderma metanevra* was recorded in 1999 in the Tennessee River approximately 2 km upstream from the mouth of the Sequatchie River (NCSMNS 86003).

We also report the presence of three rare species in the Sequatchie River: *Pleuonaia barnesiana*, *P. dolabelloides*, and *Toxolasma lividum*. *Pleuonaia barnesiana* was collected in the Sequatchie River in 1980 (MMNHC 17118), and the species was found in the Sequatchie River in the early 1900s (UMMZ 092869, UMMZ 092795). We found three live and 12 fresh dead *P. barnesiana*, the first report of this species in the Sequatchie River in over 40 years. *Pleuonaia barnesiana* has been extirpated from most of the streams it once occurred in, including the main channel Tennessee River, and it is estimated to occupy approximately 25% of its former

**Table 2.** Historical summary of freshwater mussels in Sequatchie River drainage, Tennessee. Sources: X = this study; 1 = Ortmann (1925); 2 = Hatcher and Ahlstedt (1982); 3 = Gordon (1991); 4 = Tennessee Valley Authority – unpublished data; 5 = McClung Museum of Natural History and Culture; 6 = North Carolina State Museum of Natural Sciences; 7 = Delaware Museum of Natural History; 8 = Florida Museum of Natural History; 9 = Harvard University Museum of Comparative Zoology; 10 = University of Michigan Museum of Zoology; 11 = Carnegie Museum of Natural History; 12 = Illinois Natural History Survey.

Species	Source	Species	Source
<b>Margaritiferidae</b>		<i>Leaunio vanuxemensis</i> (Lea, 1838)	X, 1, 2, 3, 4, 11, 12
<i>Margaritifera monodonta</i> (Say, 1829)	1, 3, 4, 5	<i>Lemiox rimosus</i> (Rafinesque, 1831)	6
<b>Unionidae</b>		<i>Ligumia recta</i> (Lamarck, 1819)	X
<i>Actinonaias pectorosa</i> (Conrad, 1834)	1, 10	<i>Megaloniaias nervosa</i> (Rafinesque, 1820)	X
<i>Alasmidonta viridis</i> (Rafinesque, 1820)	11	<i>Obliquaria reflexa</i> (Rafinesque, 1820)	X, 9
<i>Amblema plicata</i> (Say, 1817)	X, 3, 10, 11, 12	<i>Obovaria subrotunda</i> (Rafinesque, 1820)	1, 3, 5, 6, 9, 10, 11
<i>Cambarunio iris</i> (Lea, 1829)	X, 1, 2, 3, 4, 6, 11	<i>Pleurobema cordatum</i> (Rafinesque, 1820)	X
<i>Cyclonaias pustulosa</i> (Lea, 1831)	X, 3	<i>Pleurobema oviforme</i> (Conrad, 1834)	3, 5, 10
<i>Cyclonaias tuberculata</i> (Rafinesque, 1820)	X, 3, 4, 10	<i>Pleuonaia barnesiana</i> (Lea, 1838)	X, 1, 2, 5, 10
<i>Ellipsaria lineolata</i> (Rafinesque, 1820)	X, 3	<i>Pleuonaia dolabelloides</i> (Lea, 1840)	X, 2, 6
<i>Elliptio crassidens</i> (Lamarck, 1819)	X, 3, 5, 11	<i>Potamilus alatus</i> (Say, 1817)	X, 1, 3, 5, 9, 10, 11
<i>Epioblasma biemarginata</i> (Lea, 1857)	10	<i>Potamilus fragilis</i> (Rafinesque, 1820)	1, 11
<i>Epioblasma capsaeformis</i> (Lea, 1834)	2, 6, 10	<i>Ptychobranchnus fasciolaris</i> (Rafinesque, 1820)	X
<i>Epioblasma triquetra</i> (Rafinesque, 1820)	3, 6	<i>Pyganodon grandis</i> (Say, 1829)	6
<i>Eurynia dilatata</i> (Rafinesque, 1820)	X, 2, 3, 4, 5, 10, 12	<i>Theliderma cylindrica</i> (Say, 1817)	1, 7, 10
<i>Fusconaia cor</i> (Conrad, 1834)	10	<i>Theliderma metanevra</i> (Rafinesque, 1820)	X
<i>Fusconaia cuneolus</i> (Lea, 1840)	2, 10	<i>Toxolasma cylindrellus</i> (Lea, 1868)	6
<i>Lampsilis cardium/ovata</i>	1, 2, 3, 4, 5, 10	<i>Toxolasma lividum</i> Rafinesque, 1831	X, 6
<i>Lampsilis fasciola</i> Rafinesque, 1820	X, 1, 3, 5, 8, 10	<i>Tritogonia verrucosa</i> (Rafinesque, 1820)	X, 3, 6, 9, 10
<i>Lasmigona costata</i> (Rafinesque, 1820)	X, 13, 5, 9, 12	<i>Venustaconcha trabalis</i> (Conrad, 1834)	3, 6
<i>Lasmigona holstonia</i> (Lea, 1838)	3, 6		



range (Fitzgerald et al 2021). The USFWS was petitioned by the Center for Biological Diversity (CBD 2010) to list *P. barnesiana* as threatened or endangered under the Endangered Species Act and, in response to that petition, a survey for its occurrence across most of its historical range was conducted. However, the survey for *P. barnesiana* did not include the Sequatchie River because the species was considered extirpated in the drainage (Fraley and Dinkins 2020, Andrew Henderson, USFWS, pers. comm.). While the Clinch, Powell, and Holston River systems in the upper Tennessee River drainage represent strongholds for *P. barnesiana*, the status of populations in those watersheds varies due to localized threats associated with mining and agricultural land uses (USFWS 2020a). Remaining populations in the middle and lower Tennessee River drainage are highly fragmented due to hydrologic alteration and urban development, and as a result, natural recolonization potential in many tributaries is limited (USFWS 2020a). A decision on its listing by USFWS is expected in 2023 (Andrew Henderson, USFWS, pers. comm.). Presently, *P. barnesiana* occupies a fraction of its historical range and we agree the species deserves protected status.

We collected eight live and four fresh dead *P. dolabelloides* representing the first live individuals of this species found in the Sequatchie River. The only previous record of *P. dolabelloides* from the Sequatchie River was a complete specimen collected 11 August 1957 at Ketner Mill (NCSMNS 1022032) and a single valve collected 26 June 1980, 3.2 km north of Dunlap, Sequatchie County (Hatcher and Ahlstedt 1982). *Pleuronaia dolabelloides* was widespread in the Tennessee River drainage, occurring from the upper Clinch and Powell rivers (Virginia) downstream to the Duck and Buffalo rivers (Tennessee). In the Cumberland River drainage, the species occurred from about the Red River upstream to the vicinity of the Caney Fork (Haag and Cicerello 2016). In Kentucky, Tennessee, Alabama, Mississippi, and Virginia 25 populations have been identified, but only 17 are still extant, all in the Tennessee River drainage (Kristin Womble, Tennessee Technological University, pers. comm.). The population closest to the Sequatchie River is in the lower Paint Rock River, approximately 127 river km downstream of the Sequatchie River. *Pleuronaia dolabelloides* is listed as Endangered under the Endangered Species Act (USFWS 2013). The lower 12.9 km of the Sequatchie River has been designated as critical habitat for *P. dolabelloides*, although the species was considered extirpated from this reach (Andy Ford, USFWS, pers. comm.).

We collected 12 live and 114 fresh dead *T. lividum*, representing the first live individuals of this species reported from the Sequatchie River. The only previous collection of *T. lividum* from the Sequatchie River was on 11 August 1957 when two dead specimens (one paired specimen and one single valve) were collected immediately below Ketner Mill (NCSMNS 62878). In 2010, USFWS was petitioned by the CBD to list *T.*

*lividum* as Threatened or Endangered under the Endangered Species Act, but USFWS found listing was unwarranted (USFWS 2020b). *Toxolasma lividum* is very rare if not extirpated in Ohio (Watters et al. 2009) and is now in danger of disappearing completely in Kentucky (Haag and Cicerello 2016). The species has declined in Alabama although Garner et al. (2004) designated *T. lividum* a species of low conservation concern in the state. USFWS considers *T. lividum* to be extant in nine states (Alabama, Arkansas, Illinois, Indiana, Kentucky, Michigan, Missouri, Ohio, and Tennessee), extirpated from two states (North Carolina, Georgia), and possibly extirpated from two more (Oklahoma and Virginia) (USFWS 2020b). Historically there were 272 known populations, with 146 remaining today. Of those, 87 are small populations, confined to a limited area, with no evidence of young mussels or mussels of multiple ages (USFWS 2020b). Despite these declines, USFWS found the species had not met the threshold for protection under the ESA (USFWS 2020c). Prior to our survey, USFWS considered *T. lividum* to be extirpated from the Sequatchie River. The nearest extant population to the Sequatchie River is in the lower Paint Rock River, a direct tributary to Tennessee River in northeastern Alabama (Paul Johnson, Alabama Department of Natural Resources, pers. comm.). The Paint Rock River is approximately 127 river km downstream from the Sequatchie River and the lower reach of both rivers is impounded by reservoirs on the main channel Tennessee River.

The most common species found in our survey were *Cyclonaias tuberculata*, *Ptychobranhus fasciolaris*, *Cyclonaias pustulosa*, *Lampsilis ovata*, *Elliptio crassidens*, and *T. lividum* representing 76.8% of all live mussels found. The following species were uncommon in our survey, each represented by more than two but less than eight live individuals: *P. dolabelloides*, *Lampsilis fasciola*, *Potamilus alatus*, *Cambarunio iris*, *Lasmsgona costata*, *Leaunio vanuxemensis*, *Obliquaria reflexa*, *Megaloniaias nervosa*, and *P. barnesiana*. A single live individual was found of *Eurynia dilatata*, *Pleurobema cordatum*, *Theliderma metanevra*, and *Tritogonia verrucosa* indicating these species are extant but rare in the Sequatchie River downstream of Ketner Mill. We found three species (*Amblema plicata*, *Ligumia recta*, and *Ellipsaria lineolata*) only as dead, weathered single valves. These species may no longer be extant between river km 24.7 and 25.3 or are very rare. Prior to our survey, *L. vanuxemensis* had been documented numerous times in the Sequatchie River and as recently as 2014 (MMNHC lot no. 6437). *Leaunio vanuxemensis* was described by Lea from the Cumberland River system and this species' relationship with *Leaunio ortmanni* (Walker, 1925), Kentucky Creekshell, has been the subject of recent and ongoing taxonomic analyses (Kuehn 2009; Watters 2018; Jess Jones, USFW, unpubl. data).

In general, the mussel fauna of the Sequatchie River has largely been understudied presumably because of water quality issues related to coal mining and



wastewater discharge. The only comprehensive survey for mussels in the Sequatchie River was conducted in 1991 and the results indicated the fauna was “quite depauperate” (Gordon 1991). This may explain the general lack of interest in the Sequatchie River over the last 30 years compared to other rivers in the Tennessee River system, such as the Clinch (Ahlstedt 1991), Powell (Johnson 2011; Johnson et al. 2010), Little (Schilling et al. 2017), Hiwassee (Parmalee and Hughes 1994), Little Tennessee (Parmalee and Klippel 1984), Elk (Ahlstedt 1983), Paint Rock (Fobian et al. 2014), Duck (Ahlstedt et al. 2017; Schilling and Williams 2002), and Buffalo (Reed et al. 2019). The Sequatchie River, while not particularly remote, has few bridge crossings and is difficult to access and sample except at bridge crossings. The entire length of the main channel is bounded on both banks by private property and access to the river is restricted. In the lower 27.4 km of the main channel, there are only four bridge crossings, and at one of these (Interstate Highway 24), parking on the road shoulder is illegal which hinders river access. Further, there is little wadable habitat in the lower Sequatchie River (especially downstream of Ketner Mill) and in this lower reach depths typically range from 2–4 m during normal flows. Even though our survey effort was restricted to only a short reach of the river, we were the first to include an underwater examination of pool habitat using diving gear. Based on museum records and conversations with colleagues at several state and federal regulatory agencies, our survey effort produced the single largest collection of live mussels and dead shells to date from the Sequatchie River. The discovery of five new drainage records and rediscovery of *Toxolasma lividum*, *Pleuroaia barnesiana*, and *P. dolabelloides* demonstrates the need for additional survey work using underwater gear throughout the main channel of the Sequatchie River. Our survey also highlights the value of documenting biodiversity and setting aside areas for conservation easement.

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## Author’s Contributions

Conceptualization: GRD, BJD, RTE. Funding acquisition: BJD. Investigation: GRD, BJD, HDF, RTE, BMM. Methodology: GRD, BJD, HDF, RTE, BMM. Project administration: BJD. Validation: GRD, HDF. Visualization: GRD, BJD. Writing – original draft: GRD. Writing – review and editing: GRD.

## References

- Ahlstedt SA** (1983) The molluscan fauna of the Elk River in Tennessee and Alabama. *American Malacological Bulletin* 1: 43–50.
- Ahlstedt SA** (1991) Twentieth century changes in the freshwater mussel fauna of the Clinch River (Tennessee and Virginia). *Walkerana* 5: 73–122.
- Ahlstedt SA, Powell JR, Butler RS, Fagg MT, Hubbs DW, Novak SR, Palmer SR, Johnson PD** (2017) Historical and current examination of freshwater mussels (Bivalvia: Margaritiferidae: Unionidae) in the Duck River basin Tennessee, U.S.A. *Malacological Review* 45: 1–163.
- Bouchet P, Rocroi J** (2005) Classification and nomenclature of gastropod families. *Malacologia* 47: 1–397.
- Burch JB** (1975) Freshwater unionacean clams (Mollusca: Pelecypoda) of North America. Revised edition. Malacological Publications, Hamburg, Michigan, USA, 204 pp.
- Center for Biological Diversity** (2010) Petition to list 404 aquatic, riparian, and wetland species from the Southeastern United States as threatened or endangered under the Endangered Species Act. Letter to USA Secretary of the Interior, USA Secretary of Commerce, and Regional Director of the USA Fish and Wildlife Service, Southeast Region. April 20, 2010.
- Clarke AH** (1981) The freshwater molluscs of Canada. National Museums of Canada, Ottawa, Canada, 446 pp.
- Clarke AH** (1985) The tribe Alasmidontini (Unionidae: Anodontinae). Part II: *Lasmigona* and *Simpsonaias*. *Smithsonian Contributions to Zoology* 399: 1–101.
- Cummings KS, Mayer CA** (1993) Field guide to freshwater mussels of the Midwest. Illinois Natural History Survey, Manual 5: 1–194.
- Dawley C** (1947) Distribution of aquatic mollusks in Minnesota. *The American Midland Naturalist* 38 (3): 671–697. <https://doi.org/10.2307/2421686>
- Fitzgerald DB, Henderson AR, Maloney KO, Freeman MC, Young JA, Rosenberger AE, Kazyak DC, Smith DR** (2021) A Bayesian framework for assessing extinction risk based on ordinal categories of population condition and projected landscape change. *Biological Conservation* 253: 108866. <https://doi.org/10.1016/j.biocon.2020.108866>
- Fobian TB, Buntin ML, Holifield JT, Tarpley TA, Garner JT, Johnson PD** (2014) Freshwater mussels (Unionidae) in the Paint Rock River (Jackson, Madison, and Marshall Counties), Alabama. *Southeastern Naturalist* 13 (2): 347–366.



- Fraley SJ, Dinkins GR** (2020) A survey for *Pleurobema oviforme* and *Pleurobema barnesiana* throughout their historical range. Report prepared for the Southeastern Association of Fish and Wildlife Agencies, October 2020.
- Freshwater Mollusk Conservation Society** (2021) The 2021 checklist of freshwater bivalves (Mollusca: Bivalvia: Unionida) of the United States and Canada. Considered and approved by the Bivalve Names Subcommittee December 2020. Freshwater Mollusk Conservation Society. [https://molluskconservation.org/MServices\\_Names-Bivalves.html](https://molluskconservation.org/MServices_Names-Bivalves.html). Accessed on 2022-11-30.
- Garner JT, Blalock-Herod H, Bogan AE, Butler RS, Haag WR, Hartfield PD, Herod JJ, Johnson PD, McGregor SW, Williams JD** (2004) Freshwater mussels and snails. In: Mirarchi RA (Eds.) Alabama Wildlife. Volume 1. A checklist of vertebrates and selected invertebrates: aquatic mollusks, fishes, amphibians, reptiles, birds, and mammals. The University of Alabama Press, Tuscaloosa, Alabama, USA, 13–58.
- Gordon M** (1991) Survey of the aquatic Mollusca of the Sequatchie River and Battle Creek drainages, Tennessee. Report to Tennessee Wildlife Resources Agency, Nashville, Tennessee, USA, 21 pp.
- Haag WR** (2012) North American freshwater mussels: natural history, ecology, and conservation. Cambridge University Press, New York, USA, 505 pp.
- Haag WR, Cicerello RR** (2016) A distributional atlas of the freshwater mussels of Kentucky. Scientific and Technical Series Number 8, Kentucky State Nature Preserves Commission, Frankfort, USA, 299 pp.
- Hatcher R, Ahlstedt SA** (1982) Survey of endangered and threatened mollusks in Tennessee streams. Report to Tennessee Wildlife Resources Agency, Nashville, Tennessee, 26 pp.
- Howells RG, Neck RW, Murray HD** (1996) Freshwater mussels of Texas. Texas Parks and Wildlife Department, Inland Fisheries Division, Austin, Texas. 218 pp.
- Johnson MS** (2011) A quantitative survey of the freshwater mussel fauna in the Powell River of Virginia and Tennessee, and life history study of two endangered species, *Quadrula sparsa* and *Quadrula intermedia*. M.S. thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA, 171 pp.
- Johnson MS, Neves RJ, Henley WF** (2010) Status of the freshwater mussel fauna in the Powell River, Virginia and Tennessee. Unpublished report to U.S. Fish and Wildlife Service. Virginia Cooperative Fish and Wildlife Research Unit, Blacksburg, Virginia, USA, 77 pp.
- Johnson NA, Smith CH, Pfeiffer JM, Randklev CR, Williams JD, Austin JD** (2018) Integrative taxonomy resolves taxonomic uncertainty for freshwater mussels being considered for protection under the U.S. Endangered Species Act. Scientific Reports 8: 15892. <https://doi.org/10.1038/s41598-018-33806-z>
- Johnson PD, Bogan AE, Brown KM, Burkhead NM, Cordeiro JR, Garner JT, Hartfield DA, Lepitzki AW, Mackie GL, Pip E, Tarpley TA, Tiemann JS, Whelan NV, Strong EE** (2013) Conservation status of freshwater gastropods of Canada and the United States. Fisheries 38: 247–282.
- Jones RL, Wagner MD, Slack WT, Peyton S, Hartfield P** (2021) Guide to the identification and distribution of freshwater mussels (Bivalvia: Unionidae) in Mississippi. Second edition. Mississippi Department of Wildlife, Fisheries, and Parks, Jackson, Mississippi, USA, 344 pp.
- Kuehn K F** (2009) Exploring levels of genetic variation in the freshwater mussel genus *Villosa* (Bivalvia: Unionidae) at different spatial and systematic scales: implications for biogeography, taxonomy, and conservation. Doctoral dissertation, The Ohio State University, Columbus, Ohio, USA, 261 pp.
- Ortmann AE** (1918) The naiades (freshwater mussels) of the upper Tennessee drainage. With notes on synonymy and distribution. Proceedings of the American Philosophical Society 57: 521–626.
- Ortmann AE** (1925) The naiad-fauna of the Tennessee River system below Walden Gorge. The American Midland Naturalist 9 (7): 321–372. <https://doi.org/10.2307/2992763>
- Parmalee PW, Bogan AE** (1998) The freshwater mussels of Tennessee. University of Tennessee Press, Knoxville, Tennessee, USA, 328 pp.
- Parmalee PW, Hughes MH** (1994) Freshwater mussels (Bivalvia: Unionidae) of the Hiwassee River in east Tennessee. American Malacological Bulletin 11 (1): 21–27.
- Parmalee PW, Klippel WE** (1984) The naiad fauna of the Tellico River, Monroe County, Tennessee. American Malacological Bulletin 3 (1): 41–44.
- Reed MP, Dinkins GR, Ahlstedt SA** (2019) Freshwater mussels (Bivalvia: Margaritiferidae and Unionidae) of the Buffalo River drainage, Tennessee. Southeastern Naturalist 18 (2): 346–372.
- Schilling EM, Williams JD** (2002) Freshwater mussels (Bivalvia: Margaritiferidae and Unionidae) of the lower Duck River in middle Tennessee: a historic and recent review. Southeastern Naturalist 1 (4): 403–414.
- Schilling DE, Phipps AT, Jones JW, Hallerman EM** (2017) A survey of freshwater mussels (Unionidae) in Little River, Blount County, Tennessee. Southeastern Naturalist 16 (1): 105–116.
- Simpson CT** (1900) Synopsis of the naiades, or pearly fresh-water mussels. Proceedings of the United States National Museum 22 (1205): 501–1044. <https://doi.org/10.5479/si.00963801.22-1205.501>
- Simpson CT** (1914) A descriptive catalogue of the naiades, or pearly fresh-water mussels. Parts I–III. Bryant Walker, Detroit, Michigan, USA, xii + 1540 pp. <https://doi.org/10.5962/bhl.title.10910>
- Strayer DL, Jirka KJ** (1997) The pearly mussels of New York state. New York State Museum Memoir 26: 1–113, 27 pls
- Tennessee Department of Environment and Conservation** (2023) List of impaired and threatened waters in Tennessee. [https://www.tn.gov/content/dam/tn/enfiroment/water/watershed-planning/wr\\_wq\\_303d-2022-final.xlsx](https://www.tn.gov/content/dam/tn/enfiroment/water/watershed-planning/wr_wq_303d-2022-final.xlsx). Accessed on: 2023-04-23.
- U.S. Fish and Wildlife Service** (2013) Endangered and threatened wildlife and plants; endangered status for the Fluted Kidneyshell and Slabside Pearlymussel and designation of critical habitat. Federal Register 78 (82): 25041–25044. <https://www.govinfo.gov/content/pkg/FR-2013-04-29/pdf/2013-09975.pdf>. Accessed on: 2023-07-04.



- U.S. Fish and Wildlife Service** (2020a) Species status assessment for three freshwater mussels from the Tennessee and Cumberland River basins (*Medionidus conradicus*, *Pleurobema oviforme*, and *Pleuronaia barnesiana*), version 1.1. Asheville Ecological Services Field Office, Asheville, North Carolina, USA.
- U.S. Fish and Wildlife Service** (2020b) Species status assessment report for the Purple Lilliput (*Toxolasma lividum*), version 1.0. Asheville Ecological Field Office, North Carolina, USA, 158 pp.
- U.S. Fish and Wildlife Service** (2020c) Endangered and threatened species: 12-month finding for Purple Lilliput; Longsolid and Round Hickorynut and designation of Critical Habitat. 75 pp. <https://www.govinfo.gov/content/pkg/FR-2020-09-29/pdf/2020-17015.pdf>. Accessed on: 2023-07-04.
- U.S. Fish and Wildlife Service** (2023) Environmental Conservation Online System. <https://www.ecos.fws.gov/ecp>. Accessed on: 2023-04-23.
- Vidrine MF** (1993) The historical distributions of freshwater mussels in Louisiana. Gail Q. Vidrine collectibles, Eunice, Louisiana, USA, 225 pp.
- Watters GT** (2018) A preliminary review of the nominal genus *Villosa* of freshwater mussels (Bivalvia, Unionidae) in North America. *Visaya*, Supplement 10: 1–140.
- Watters GT, Hoggarth MA, Stansbery DH** (2009) The freshwater mussels of Ohio. The Ohio State University, Columbus, Ohio, USA, 421 pp.
- Williams JD, Bogan AE, Garner JT** (2008) The freshwater mussels of Alabama and the Mobile Basin in Georgia, Mississippi, and Tennessee. University of Alabama Press, Tuscaloosa, Alabama, USA, 908 pp.
- Williams JD, Butler RS, Warren GL, Johnson NA** (2014) Freshwater mussels of Florida. University of Alabama Press, Tuscaloosa, Alabama, USA, 498 pp.
- Williams, JD, Bogan AE, Butler RS, Cummings KS, Garner JT, Harris JL, Johnson NA, Watters GT** (2017) A revised list of the freshwater mussels (Mollusca: Bivalvia: Unionida) of the United States and Canada. *Freshwater Mollusk Biology and Conservation* 20: 33–58.